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Approaches to Enhance Salt Stress Tolerance in Wheat

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Abstract

Wheat is consumed as a staple food by more than 36% of world population. Wheat provides nearly 55% of the carbohydrates and 20% of the food calories consumed globally. The productivity of wheat is often adversely affected by salt stress which is associated with decreased germination percentage, reduced growth, altered reproductive behavior, altered enzymatic activity, disrupted photosynthesis, damage of ultrastructure of cellular components, hormonal imbalance, and oxidative stress. Different approaches have been adopted to improve plant performance under salt stress: introduction of genes, screening of better performing genotypes, and crop improvement through conventional breeding methods which are often not so successful and suitable due to time-consuming or reduction of plant vigor with the succession of time. Uses of exogenous phytoprotectants, seed priming, nutrient management, and application of plant hormone are convenient for improving plant performances. This chapter reviews the mechanism of damage of wheat plants under salt stress and also the recent approaches to improve growth and productivity of salt-affected wheat plants emphasizing the use of exogenous phytoprotectants from the available literature.

Keywords: abiotic stress, antioxidant defense, cereal crop, stress tolerance, phytohormones

1. Introduction

Worldwide, more than 20% of the cultivable land is affected by salinity. Due to climate change and anthropogenic activities, the salt affected area is tended to increase day by day [1]. Abiotic stresses (including salinity) are accountable for more than 50% yield reduction [2]. In contrary, due to rapid increase of global population, food production should be increased by more than 70% by 2050 [3]. Wheat (*Triticum* spp.) ranks first in the world's grain production. Wheat is consumed as staple food by more than 36% of world population. Wheat provides nearly 55% of the carbohydrates and 20% of the food calories consumed globally [4, 5]. The productivity of wheat is often adversely affected by salt stress. The yield of wheat starts to decline at 6–8 dS m^{-1} [6]. Under salt stress, hyperosmotic and hyperionic (ion toxicity) stresses occur due to low water potential of soil and excess sodium ion accumulation within the plant. Ionic stress is also associated with nutritional imbalance [7, 8]. Decreased germination percentage, reduced growth, altered reproductive behavior, and reduced yield are general effects on plants under salt stress [9]. Altered enzymatic activity, disrupted photosynthesis, oxidative stress, disrupted biomembrane structure and function, damage of ultrastructural cellular components, and hormonal imbalance are some reasons for decreasing overall growth and development of plants under salt stress [10–12].

Salt stress tolerance is a polygenic trait regulated by multiple factors/genes. Exclusion of Na$^+$, cytosolic K$^+$ retention and maintenance of K$^+$/Na$^+$ homeostasis, osmotic adjustment, transpiration efficiency, and enhanced antioxidant defense system are vital for better plant performance under salt stress [13–15]. Different approaches have been adopted to improve plant performance under salt stress; introduction of genes, screening of better performing genotypes, and crop improvement through conventional breeding methods which are often not so successful and not suitable due to time consuming or reduction of plant vigor with the succession of time. Uses of exogenous phytoprotectants, seed priming, nutrient management, and application of plant hormones are convenient for improving plant performances. These approaches are being also popular for stress management practices including the salt stress [16–25]. In this chapter, we will review the recent research works on different approaches of salt stress tolerance in wheat plants emphasizing the use of exogenous phytoprotectants.

2. Wheat responses to salt stress

Salinity is one of the most devastating abiotic stresses having enormous negative effects on morphological, physiological, and biochemical attributes of plant including germination, growth, water uptake, photosynthesis, nutrient uptake, enzymatic activities, and yield. A number of studies revealing the effects of salt stress on different wheat cultivars, among which some are tolerant and some susceptible to salt stress. Higher salinity causes lower germination rate, photosynthesis, transpiration, and higher accumulation of Na$^+$ and Cl$^-$ ions which disturb the normal metabolic processes of wheat plants (**Table 1**; **Figure 1**).

Cultivars	Salinity level	Effects	Reference
MH-97 and AUQAB-2000	15 dS m^{-1}	• Decreased DW and FW of root and shoot • Increased activities of catalase (CAT) and super-oxide dismutase (SOD) • Increased protein and AsA contents	Afzal et al. [43]
KRL-19 and WH-542	100 mM NaCl, 6 d	• Decreased leaf relative water content (RWC) and leaf osmotic potential • Increased H_2O_2, malondialdehyde (MDA) contents and electrolyte leakage • Increased activities of CAT, glutathione reductase (GR), SOD, ascorbate peroxidase (APX), and peroxidase (POD) • Increased Na^+ accumulation, decreased K^+ accumulation, and increased K^+/Na^+ ratio	Mandhania et al. [37]
S-24 and MH-97	150 mM NaCl, 7 d	• Decreased shoot and root FW • Decreased grain yield, 1000 grain weight and transpiration rate • Increased Na^+ and Cl^- contents and decreased K^+ and Ca^{2+} contents in both leaf and root	Arfan et al. [19]
MH-97	150 mM NaCl	• Increased mean germination time • Decreased FW and DW of shoot and leaf area • Increased Na^+ and Cl^- contents, and decreased K^+ and Ca^{2+} contents and K^+/Na^+ ratio • Decreased NO_3^- and PO_4^{3-} contents	Wahid et al. [35]
Inqlab-91 and SARC-1	125 mM NaCl, 7 d	• Increased Na^+ and Cl^- contents, and decreased K^+ and Ca^{2+} contents • Decreased FW and DW	Afzal et al. [28]
Banysoif 1	320 mM NaCl, 155 d	• Decreased contents of photosynthetic pigments and rate of transpiration • Increased Pro content and decreased amino acid content • Higher accumulation of Na^+ in root, shoot, and spike	Tammam et al. [36]
Hirmand, Chamran, Hamoon, Bolani, Sorkhtokhm, and Kavir	12.5 dS m^{-1}	• Delayed and decreased seed germination • Increased Na^+ accumulation and decreased K^+ content in both shoot and root	Akbarimoghaddam et al. [30]
Tatara-96, Ghaznavi-98, Fakhri Sarhad, Bakhtawar-92, Pirsabaq-2004, and AUQAB-2000	120 mM NaCl	• Decreased shoot FW and DW • Increased Na^+ and K^+ contents, and decreased K^+/Na^+ ratio	Jamal et al. [32]

Cultivars	Salinity level	Effects	Reference
Tajan, Rasoul, Atrak, and Kouhdasht	16 dS m^{-1}	• Decreased grain yield and 1000-grain weight • Increased Na$^+$ and Cl$^-$ contents, and decreased K$^+$ and Ca^{2+} contents	Asgari et al. [40]
Caxton	200 mM NaCl, 8 d	• Decreased germination percentage	Fuller et al. [31]
MH-97 and Inqlab-91	15 dS m^{-1}	• Decreased net CO$_2$ assimilation rate, stomatal conductance, and transpiration rate • Decreased shoot FW	Iqbal and Ashraf [44]
Dan-4589	80 mM (NaCl and Na$_2$SO$_4$ at a molar ratio of 9:1)	• Increased Na$^+$ content and decreased K$^+$ content • Decreased rate of photosynthesis and transpiration • Decreased chl content and intercellular CO$_2$ concentration	Guo et al. [33]
HD 2329 and Kharchia-65	200 mM NaCl, 9 d	• Decreased activity of SOD and increased activities of POD, APX, CAT, and GR	Singh et al. [45]
Transgenic lines: T1, T4, and T6	200 mM NaCl, 4 d	• Decreased net photosynthetic rate, stomatal conductance, and increased intercellular CO$_2$ concentration in leaves • Decreased chl and carotenoid contents	Tian et al. [46]
Yangmai 16	0.75% NaCl	• Higher accumulation of Na$^+$ and decreased K$^+$/Na$^+$ ratio	Zhang et al. [47]
Jimai 22	100 mM NaCl, 10d	• Increased MDA content • Increased activities of SOD, POD, CAT, GR, APX, and dehydroascorbate reductase (DHAR)	Zou et al. [34]

Table 1. Responses of *T. aestivum* plants to salt stress.

2.1. Germination

Germination is one of the most important and vital processes of plant life cycle. It is the determinant of the subsequent growth and yield characteristics of plants. Available literature showed that wheat seeds tended to germinate at a lower rate and consumed longer time when exposed to salt stress. The reasons underlying this fact are higher concentrations of salt create lower osmotic potential of germination media which hampers the imbibition of water by seed, creates an imbalance in the normal activities of enzymes responsible for nucleic acid and protein metabolism, causes hormonal imbalance, and deteriorates the food reserves of seed [26]. But, there are many other factors related to the plant and environment which also have effects on germination process. These include age of seed, seed dormancy, seed coat hardness, seed polymorphism, vigority of seedling, moisture, temperature, gasses, and light, etc. [27]. Germination also varies with different cultivars considering whether tolerant or susceptible type. Afzal et al. [28] reported that under saline condition (125 mM NaCl), wheat seeds required longer time for germination than seeds under nonsaline condition. Similar results were presented by Ghiyasi et al. [29] with upto 16 dS m^{-1} salinity levels. Mean germination

time increased and germination rate and germination index decreased with increasing levels of salinity. Akbarimoghaddam et al. [30] reported delayed and decreased wheat seed germination at 12.5 dS m^{-1} salinity. Fuller et al. [31] also showed a distinct relationship of the decreasing germination percentage with increasing salinity levels (upto 200 mM NaCl).
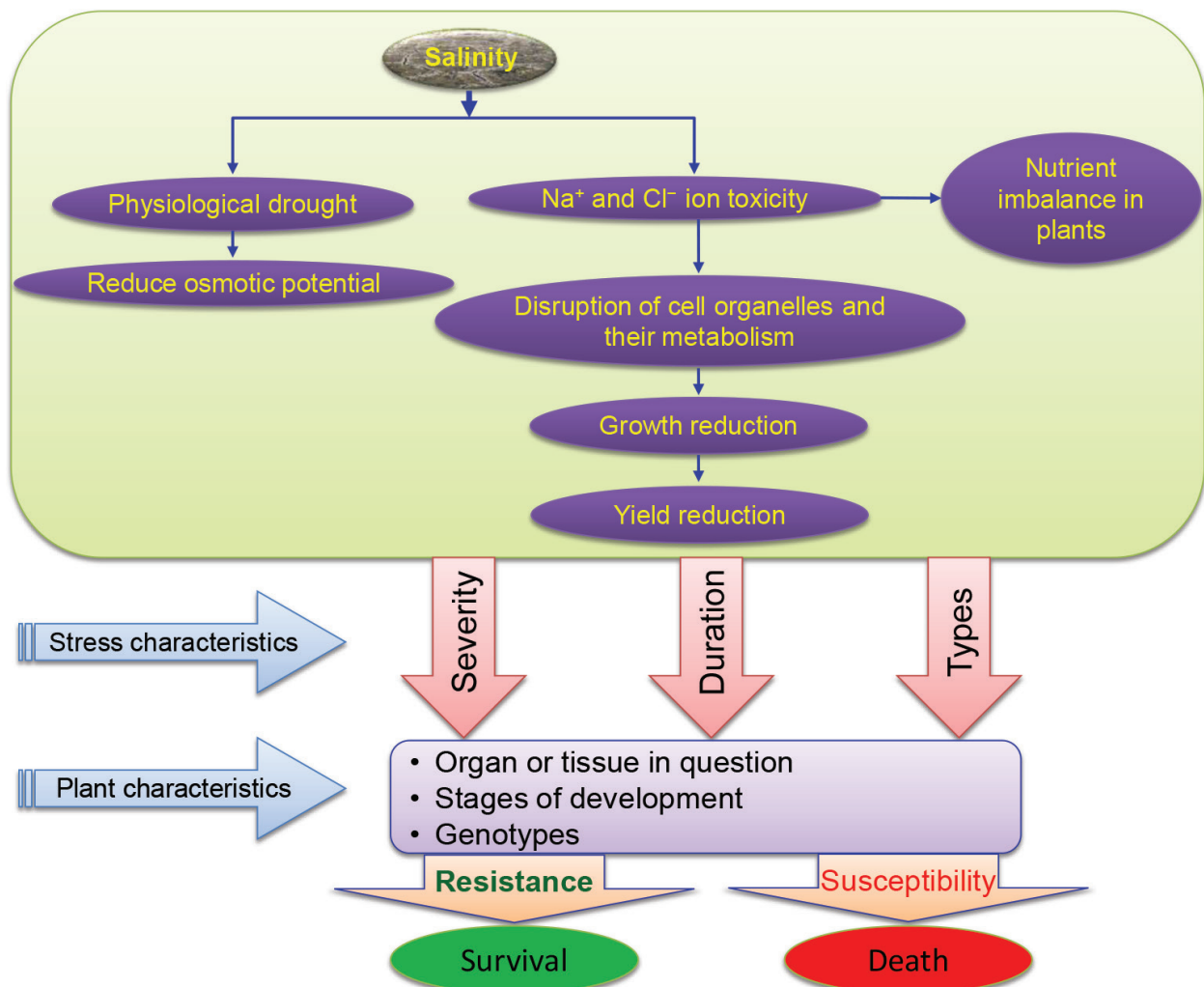

Figure 1. General scheme of salt stress responses and adaptation in plants.

2.2. Growth

Salt stress affects the growth of wheat seedlings remarkably. Root and shoot length, plant height, leaf area, number of effective tillers, and number of spike, etc. are considered to be growth parameters. There are many reports that show the evidence of hampering these characters under saline condition. Moreover, in the seedling stage, plants are more sensitive to adverse environmental conditions. So, in this stage, high salinity may even cause death of seedlings. Fresh and dry mass of shoot, leaf area, etc. of both sensitive and tolerant cultivars declined under salt stress in wheat seedlings [19]. Length, fresh weight (FW), and dry weight (DW) of both root and shoot of wheat seedlings were negatively affected by different levels

of salinity as 150 mM NaCl [20]; 125 mM NaCl [28], 16 dS m^{-1} salinity [29], and 120 mM NaCl [32]. Guo et al. [33] showed decreased growth of leaves of wheat seedlings and roots under salt stress, compared to the nonstressed control. Similarly, reduced shoot length, root length, wet weight, and DW after 10 d with 100 mM NaCl treatment were observed by Zou et al. [34].

2.3. Photosynthesis

Photosynthesis is the major physiological process for plant survival and greatly influenced by environmental factors. As salinity reduces water potential and increases accumulation of Na$^+$ and Cl$^-$ ions in the chloroplast, the rate of photosynthesis gets inhibited [26]. According to the experiment conducted by Arfan et al. [19], exposure to salt stress reduced the transpiration rate, net CO_2 assimilation rate, stomatal conductance, and substomatal CO_2 concentration of both cultivars. Similarly, net photosynthetic rate, transpiration rate, stomatal conductance, and substomatal CO_2 concentration were decreased significantly at 150 mM NaCl stress [35]. Tammam et al. [36] reported that amount of photosynthetic pigments were significantly deceased in seedlings under 320 mM NaCl stress. Reduction of stomatal conductance and transpiration rate were also reported by Guo et al. [33]. Significant decrease of chlorophyll (chl) content was recorded in wheat seedlings at 100 mM NaCl, for 10 d [34].

2.4. Water relation

Availability of moisture in plants is a crucial factor for all physiological and metabolic processes of plants. Higher salt concentrations induce osmotic stress to plants, which ultimately causes low water potential. Relative water content (RWC) declined by 3.5 and 6.7%, compared to their controls in the salt-tolerant and salt-sensitive cultivars, respectively, after 6 d of 100 mM NaCl exposure [37]. They also reported lowering of osmotic potential with increasing salt concentrations. Arfan et al. [19] showed reduced water use efficiency (WUE) of both sensitive and tolerant cultivars under saline condition. Leaf water potential also decreased under salt stress of 150 mM NaCl [35] and 16 dS m^{-1} [38]. Percentage of water content decreased in root, but increased in shoot and spike of Banysoif 1 cultivar of wheat [36]. Lv et al. [39] recorded lower RWC in leaves of *T. monococcum* seedlings exposed to salt stress of 320 mM NaCl.

2.5. Cellular damage

Inconsistent growth and improper uptake of water and nutrients ultimately result in deterioration of cell membrane properties of plants. Lipid peroxidation, accumulation of hydrogen peroxide (H_2O_2), and increased membrane permeability are some common phenomenon of wheat seedlings under salt stress. Mandhania et al. [37] reported higher damage of cellular membranes of salt-sensitive cultivar due to higher H_2O_2 accumulation and lipid peroxidation which enhanced the electrolyte leakage compared to the tolerant one. Higher accumulation of H_2O_2 in salt-stressed wheat seedlings was also proved by Wahid et al. [35] which was responsible for the increased relative membrane permeability. Lipid peroxidation increased by 68% under NaCl treatment of 100 mM for 10 d compared to control [34].

2.6. Ion uptake

Higher accumulation of Na^+ and Cl^- ions interferes with the uptake of other necessary ions which disturbs plant processes. Salt-sensitive cultivars tend to uptake more Na^+ compared to the tolerant one and this uptake rate increases with increasing concentration of salt [37]. Lower accumulation of NO_3^- and PO_4^{3-} ions were recorded by Wahid et al. [35]. They also reported higher uptake of Na^+ and Cl^-, and reduced uptake of K^+ and Ca^{2+} by salt stressed wheat seedlings. Similar results were published by Afzal et al. [28] in wheat seedlings exposed to 125 mM of NaCl stress for 7 d. But, Jamal et al. [32] reported increased uptake of Na^+ and K^+ both ions, and decreased K^+/Na^+ ratio in wheat shoots when exposed to 120 mM of NaCl. On the other hand, both Asgari et al. [40] and Afzal et al. [41] recorded significant decrease of K^+ uptake under saline condition (15–16 dS m^{-1}). Under medium salinity, higher accumulation of both Na^+ and Cl^-, and lower uptake of K^+, Ca^{2+}, and Zn^{2+} ions were reported by Guo et al. [33].

2.7. Yield

All the above mentioned factors are responsible directly or indirectly for the subsequent yield reduction of wheat plants. Yield of almost all crops, except some halophytes, is reduced under salt stress. The amount of yield reduction may vary upon the sensitivity and tolerance of the wheat cultivars. Chinnusamy et al. [42] indicated that above the threshold level of salinity of 6 dS m^{-1}, wheat yield can reduce at a rate of 7.1% per dS m^{-1} increase of salinity. Asgari et al. [40] reported that the spikes number per plant, spike length, number of spikelets per spike, straw weight, grain yield, 1000-grain weight, and harvest index declined with the increasing level of salinity, which ultimately caused yield loss. A significant decrease in number of grains per spike, 1000-grain weight, and grain yield were reported in both tolerant and sensitive cultivars of wheat seedlings under 15 dS m^{-1} salinity [41].

3. Salt-induced oxidative stress in wheat

Salt stress can lead to stomatal closure, which reduces CO_2 availability in the leaves and inhibits carbon fixation, exposing chloroplasts to excessive excitation energy which in turn increase the generation of reactive oxygen species (ROS) such as superoxide ($O_2^{\bullet-}$), H_2O_2, hydroxyl radical (OH•), and singlet oxygen ($^1O_2$) [26, 48, 49] (**Figure 2**). Since, salt stress is complex and imposes a water deficit because of osmotic effects on a wide variety of metabolic activities [50]; this water deficit leads to the formation of ROS that are highly reactive and may cause cellular damage through oxidation of lipids, proteins, and nucleic acids [51]. If there is a serious imbalance in any cellular compartment between the production of ROS and antioxidant defense, oxidative stress and damage occur [52] (**Figure 2**). Enhanced production of ROS under salinity stress induces phytotoxic reactions such as lipid peroxidation, protein degradation, and DNA mutation [53]. When a plant faces harsh conditions, ROS production overcomes scavenging systems and oxidative stress will burst. In many plant studies, it was observed that production of ROS increased under saline conditions [54]

and ROS-mediated membrane damage has been demonstrated to be a major cause of the cellular toxicity by salinity in different crop plants ([49]; **Table 2**). Long-term salinity treatments (5.4 and 10.6 dS m^{-1}, 60 d) caused significant increase in H_2O_2 and lipid peroxidation in wheat seedlings, which were higher in salt-sensitive cultivar than salt-tolerant cultivar [55]. Increased lipid peroxidation and H_2O_2 levels with increased salinity stress in *T. aestivum* were observed in our study [24]. Wheat seedlings exposed to 300 mM NaCl resulted in 60 and 73% increase in H_2O_2 and MDA contents. Salt stress also decreased ascorbic acid (AsA) content by 52%. According to Zou et al. [34], *T. aestivum* leaves showed 35% increase in MDA content upon 100 mM NaCl treatment for 5 d which further increased by 68% after 10 d of treatments. Rao et al. [56] observed dose dependent increase in lipid peroxidation in wheat exposed to salt (2, 4, 8, and 16 EC) and these effects were variable among the cultivars. They found increased MDA content in cultivars, ZARDANA (55.9%), ROHTAS-90 (42.26%), SAUGHAT-90 (51%), and SHAHEEN-94 (52%), and hence they were designated as salt sensitive, whereas PUNJAB-85 (33%), BHAKAR 2002 (35%), PIRSBAK-05 (31%), and AUQAB (28%) showed decreased levels of lipid peroxidation and were categorized as salt tolerant [57].
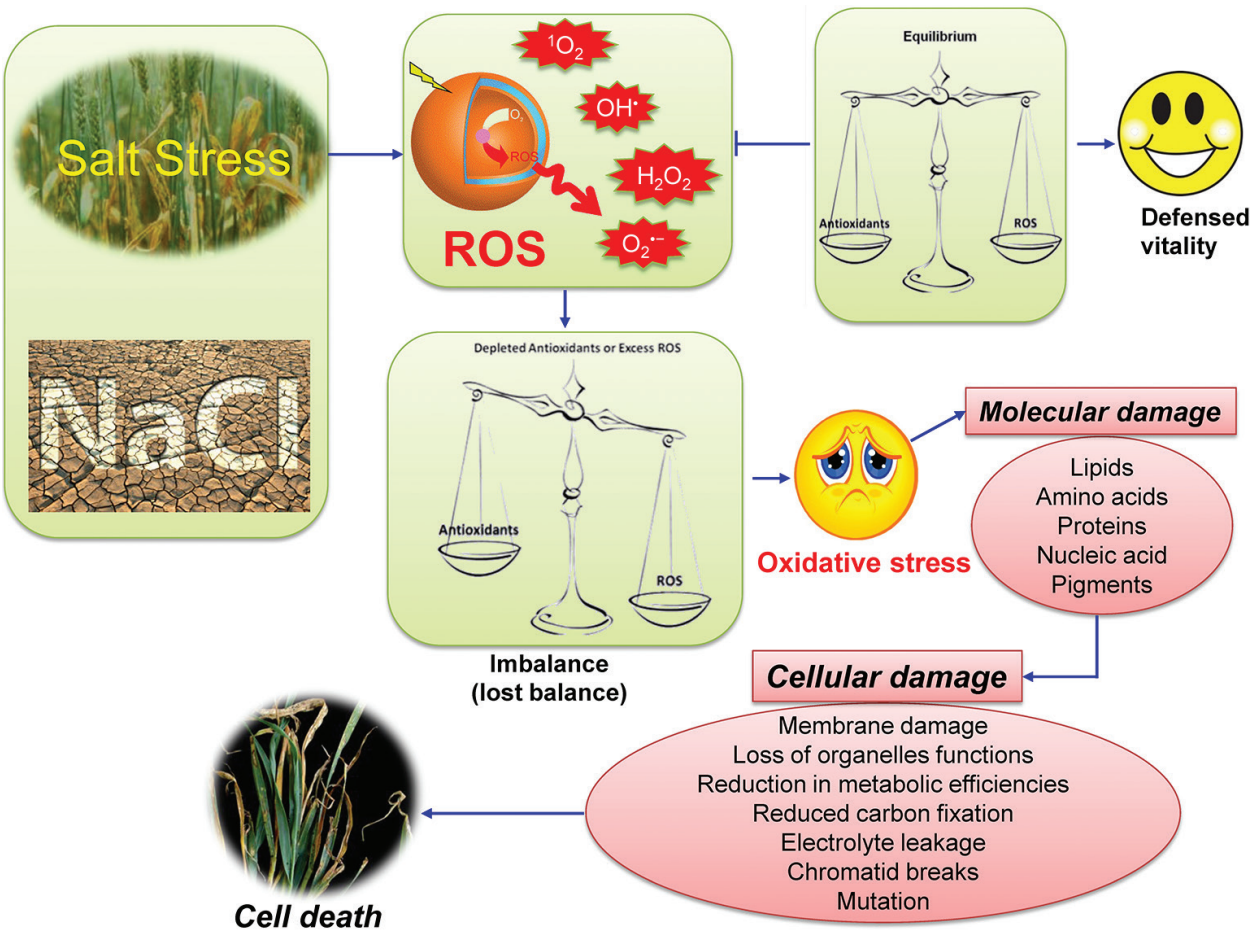

Figure 2. Generalized scheme of salt-induced oxidative stress in plants.

Name of cultivars	Dose and duration of salt	Level of oxidative stress	References
Pradip	300 mM NaCl, 4 d	• Increased H_2O_2 and MDA content by 60 and 73%, respectively	Hasanuzzaman et al. [24]
Kharchia-65	6.85 dS m^{-1} NaCl	• Enhanced lipid peroxidation (TBARS) and H_2O_2 content by 21 and 38%, respectively	Sairam and Srivastava [58]
Jimai 22	100 mM NaCl, 10 d	• MDA content increased by 68.3% in leaves	Zou et al. [34]
ZARDANA BAKHAR-2002, SAUGHAT-90, and AUQAB-2000	16 dS m^{-1} NaCl	• Lipid peroxidation enhanced by 56, 35, and 51% in ZARDANA BAKHAR-2002, and SAUGHAT-90 cultivars, respectively • DPPH radical scavenging activity decreased by 47% in AUQAB-2000	Rao et al. [56]
Kızıltan-91	100 mM NaCl, 5 d	• Increased lipid peroxidation level by 53%	Seckin et al. [59]
Yongliang 4	150 mM NaCl, 16 h	• Increased MDA content in leaves by 50%	Zhang et al. [60]
Altındane	100 mM NaCl, 3 d	• Elevated MDA, $O_2^{\bullet-}$, and H_2O_2 contents by 26, 43, and 53%, respectively	Gorcek and Erdal [61]
Waha	150 mM NaCl, 14 d	• MDA content increased by 10% and fourfold increase of H_2O_2 content	Fercha [62]
WenmaiNo.6	150 mM NaCl, 4 d	• Increased MDA, $O_2^{\bullet-}$, and H_2O_2 contents by 47, 38, and 33%, respectively	Qiu et al. [63]
	150 mM NaCl, 72 h	• Increased MDA and H_2O_2 contents by 52 and 47%, respectively	Genişel and Erdal [64]

Table 2. Salt-induced oxidative stress in *T. aestivum* compared to control.

Plants have antioxidative mechanism to fight against stress under adverse conditions. So, they naturally produce higher amount of antioxidant enzymes, e.g., CAT, GR, SOD, APX, POD, and DHAR, etc. to minimize the damage due to stress. Mandhania et al. [37] reported that the activities of CAT, GR, SOD, APX, and POD enzymes increased with the increasing concentration of salt irrespective to tolerance or sensitivity of the cultivar. In another experiment with sensitive and tolerant type of cultivars, ascorbic acid (AsA) content and activities of SOD, CAT, and POD also increased in both under salt stress [20]. But, in another experiment by Singh et al. [45], SOD activity was recorded to decrease with the increasing concentration of salt in a salt-sensitive cultivar named HD2329; while activities of POD, APX, CAT, and GR increased with the same treatments. Significantly, higher activities of SOD and POD were presented by Zou et al. [34] with NaCl treatment of 100 mM for 10d, but they showed insignificant increase of CAT and APX activities, and significant decrease of GR and DHAR activities under same treatment. The activities of SOD and POD were increased with increasing the levels of salt concentrations in *T. monococcum* seedlings [39].

4. Salt tolerance approaches

Considering the adverse effects of salt stress in wheat plant, biologists are trying to find out the salt-tolerant strategies in plants by different approaches. Many researchers found positive effect in using exogenous phytoprotectants in alleviating salt-induced damages in wheat. In this section, some of the evidences are discussed.

4.1. Use of osmoprotectants

To prevent the adverse effects of various environmental stresses including salt stress, plants demonstrate a variety of adaptive mechanisms both at the cellular and organismal levels. Under salt stress conditions, to cope with the salt-induced osmotic, ionic as well as oxidative stresses, plant synthesizes and accumulates organic compatible solutes or osmolytes [48, 65, 66]. Accumulation of these compatible solutes is one of the most important physiological strategies employed by plants under salt stress conditions. Osmoprotectants or osmolytes are small, highly soluble, uncharged, and nontoxic organic molecules which help to survive organisms in extreme osmotic stresses. Osmoprotectants comprise of (i) α-amino acids such as proline (Pro) and ectoine; (ii) ammonium compounds such as glycine betaine (GB), β-alanine betaine, dimethylsulfoniopropionate (DMSP), and choline; and (iii) polyols, sugars, and sugar alcohols such as trehalose (Tre), sorbitol, and mannitol, etc. These osmoprotectants perform vital functions in osmotic adjustment, stabilizing proteins and membranes. Thus, enhanced salt stress tolerance is observed in plants overexpressing the osmoprotectants biosynthetic and metabolic genes. Enhanced salt exposure causes increased biosynthesis of osmoprotectants (Pro, GB, Tre, ecotine, and sorbitol, etc.) which provides enhanced osmotic stress tolerance generated from salt stresses [67, 68] (**Table 3**). For mitigating salt-induced damages, in recent decades, the use of exogenous osmoprotectants has been found effective [12, 69]. Several research findings demonstrated that the use of osmoprotectants provided significant protection against adverse effects of salt stresses in *T. aestivum* seedlings (**Table 3**). At the same time, several research studies proved Pro as a potent protectant against the adverse effects of salt. Proline acts not only in osmotic adjustment as a compatible solute, but also in scavenging ROS, chelating metal, activating detoxification pathways, balancing cells redox status, buffering cytosolic pH, storing energy (carbon and nitrogen), stabilizing subcellular membranes and structures including photosystem II (PS II), and as signaling molecule [70–74]. Raza et al. [75] demonstrated the effect of exogenous GB (50 mM and 100 mM) in moderately salt-sensitive (MH-97) and salt-tolerant (S-24) wheat cultivars grown under salt stress (15 dS m^{-1} NaCl). Glycine betaine treatment ameliorated the salt-induced photosynthetic reduction as well as increased the photosynthetic capacity, water use efficiency, and osmotic adjustment where salt-tolerant (S-24) cultivar showed better performance against salt stress compared to moderately salt-sensitive (MH-97) cultivar. Later, with the same experimental procedure, they again suggested that the exogenous GB modulated the activities of antioxidant enzymes such as SOD, CAT, and POD which contributed significantly to salt stress tolerance in *T. aestivum* [76]. It has been reported that accumulation of Pro protects *T. aestivum* from the salt-induced damages by maintaining a higher K$^+$/Na$^+$ ratio and reducing ionic toxicity [38], increasing the major antioxidant enzymes (CAT, APX, SOD, and POD) activities [77]. In *T. aestivum*, GB (10 mM and

30 mM) supplementation with salt stress (150 mM NaCl) increased the germination percentage, shoot Ca content, total chl content, and thus confer salt stress tolerance [78]. Khan et al. [79] reported that increased grain yield in *T. aestivum* associated with the increased Pro, chl content and K$^+$/Na$^+$ ratio. Overexpression of GB in transgenic *T. aestivum* lines T1, T4, T6, and Shi 4185 (wild type line) caused enhanced salt stress (200 mM NaCl) tolerance by enhancing ROS scavenging, osmotic adjustment and regulating ion homeostasis [80]. Salt stresses (10 dS m^{-1} NaCl) were imposed in two wheat cultivars (cv. Seher and Lasani). In both wheat cultivars, salt stresses caused significant reduction in the germination percentage, chl contents and growth. Exogenous Pro (50 and 100 mM) application alleviated the adverse effects of salt stress by improving the germination percentage, seedling growth and chl contents of wheat plants but 100 mM Pro was found more effective compared to 50 mM Pro [81]. Mahboob et al. [82] reported that the supplementation of Pro (50 and 100 mM) ameliorated the salt (60 and 120 mM NaCl) induced reduction of plant growth, photosynthetic pigments and ionic balance by increasing shoot and root length, chl *a, b* contents, FW and DW of seedlings and endogenous Pro, GB, and K$^+$/Na$^+$ ratio in *T. aestivum* seedlings. Exogenous Pro (60 ppm) upregulated the endogenous hormones (gibberelic acid (GA$_3$) and indole acetic acid (IAA)), ammonium compounds (GB and choline) and downregulated the MDA content and growth inhibitor abscisic acid (ABA) in salt stressed *T. aestivum* [83]. Salt (50, 150, and 300 mM) induced disruption of photosynthetic pigments and protein polypeptide synthesis in *T. aestivum* were prevented by the exogenously applied Pro (50 ppm) and at the same time by protecting the turnover machinery of proteins [84]. Besides osmotic adjustment, GB is also involved in ROS scavenging, stabilizing macromolecules (nucleic acids, proteins, and lipids) and various components of photosynthetic machinery such as PS II complexes and RuBisCO and acts as reservoir of carbon and nitrogen sources [85–87]. Upon salt exposure (150 mM NaCl), reduced lipid peroxidation, increased glutathione (GSH) and GB concentrations, enhanced plasma membrane protection, increased cell solute potential and improved ion homeostasis were observed when caryopsis of *T. aestivum* were primed with GB (25, 50, 100 mM) [88]. Increasing the K$^+$/Na$^+$ and Ca$^+$/Na$^+$ ratios, reducing MDA content, protecting photosynthetic apparatus, improving plasma membrane integrity and stabilizing macromolecules (proteins, PS II and transporters) GB (20 mM) imparted in salt stress tolerance in *T. aestivum* [83]. Exogenous GB (5 mM) application improved chl *a*, total chl and K$^+$ content of roots, increased root length, plant height, FW and DW of *T. aestivum* under salt stresses (100 and 200 mM NaCl) [89]. Rao et al. [57] suggested that the enhanced production of Pro and GB in six salt-tolerant cultivars (*T. aestivum* cv. AUQAB-2000, PUNJAB-85, PIRSABAK-05, BAKHAR-2002, FARKHARE-SARHAD and KAGHAN-94) alleviated the damaging effects of salt stress by activating their antioxidant enzymes. Endogenous Pro and GB mediated salt stress (8 EC, 16 EC) mitigation in fifteen *T. aestivum* cultivars were further reported by Rao et al. [57]. They suggested that the five cultivars of wheat (SEHAR-2006, LU26-CTR, NARC-2009, BARS-2009, PIRSABAK-09) showed obvious salt stress tolerance by increasing the production of Pro and GB. Yan and Zheng [90] demonstrated that pretreatment with Tre (2, 20, and 40 mM) alleviated the adverse effects of salt stress (3 g L^{-1} NaCl) in *T. aestivum* cv. Yangmai-19. Various beneficial effects were observed in different physiological parameters. Increased relative growth rate, relative chl content, N content, DW and biomass plant^{-1} were observed with Trehalose supplementation. Trehalose application also improved Pro accumulation, K$^+$ accumulation and K$^+$/Na$^+$ ratio. In addition,

Tre has functions in stabilizing the biomolecules and structures like membrane lipids, proteins under salt stress [91–93]. Salt-sensitive wheat cultivar (*T. aestivum* cv. Kızıltan-91) under salt stress (100 mM NaCl) showed physiological alteration. However, pretreatment with exogenous mannitol (100 mM) reversed the deleterious salt effects by increasing antioxidant enzymes (such as SOD, POD, CAT, APX, and GR) activities, appearance of SOD and POD isozyme activity bands and reducing lipid peroxidation [59].

Cultivars	Salinity doses and duration	Doses of osmolytes	Protective effects	References
ESW-9525 and kherman	60 and 120 mM NaCl, 7 d	50 and 100 mM Pro, foliar spray	• Increased shoot and root length • Increased FW and DW of seedlings • Increased chl *a*, *b* contents • Improved Pro, GB, K^+ contents, and K^+/Na^+ ratio	Mahboob et al. [82]
Seher and Lasani	10 dS m^{-1} NaCl, 6 d	50 mM and 100 mM Pro, foliar spray	• Improved gaseous exchange parameters (net CO_2 assimilation rate, stomatal conductance, substomatal CO_2 concentration, and transpiration rate) • Increased chl *a*, *b*, and total chl contents	Talat et al. [81]
MH-97 and S-24	15 dS m^{-1} NaCl	50 mM and 100 mM GB, foliar spray	• Improved WUE • Increased photosynthetic capacity • Increased stomatal conductance	Raza et al. [75]
Kızıltan-91	100 mM NaCl, 5 d	100 mM mannitol, pretreatment, 24 h	• Increase activities of SOD, POD, CAT, APX, and GR • Reduced lipid peroxidation and membrane damage	Seckin et al. [59]
Gomeza 7	150 mM NaCl, 38 d	25, 50, and 100 mM GB, caryopsis priming, 24 h	• Reduced lipid peroxidation • Increased the GSH and GB concentrations • Enhanced plasma membrane (PM) protection • Increased the cell solute potential • Improved ion homeostasis	Salama et al. [88]
Sakha 93 and Gimmeza7	10.04 dS m^{-1} (soil), 35–65 d 7.33 dS m^{-1} (irrigation water), 35–65 d	60 ppm Pro, foliar spray	• Increased chl *a* and *b* • Increased endogenous hormones (GA and IAA) • Increased GB and choline • Decreased MDA content and ABA	Hendawey et al. [83]
Sakha 93 and Gimmeza7	10.04 dS m^{-1} (soil) 7.33 dS m^{-1} (irrigation water), 35 to 65 d	20 mM GB, foliar spray	• Increased K^+/Na^+ and Ca^+/Na^+ ratios • Improved K, Ca, and Zn contents • Reduced MDA content • Protected photosynthetic apparatus • Improved PM integrity and stabilization of macromolecules (proteins, PS II, and transporters)	Hendawey et al. [83]

Cultivars	Salinity doses and duration	Doses of osmolytes	Protective effects	References
Yangmai-19	3 g L^{-1} NaCl	2, 20, and 40 mM Tre, seed soaking	• Increased relative growth rate, relative chl content, N content, DW, and biomass per plant • Increased Pro accumulation • Increased K$^+$ accumulation and K$^+$/Na$^+$ ratio, and decreased Na$^+$ content	Yan and Zheng [90]
S-24 and MH-97	150 mmol L^{-1} NaCl, 15 d	10 and 30 mM of GB, presoaking	• Increased germination percentage • Increased shoot Ca content • Increased total chl content	Akhter et al. [78]
Gomeza	150 mM NaCl, 21 d	5 and 10 mM choline, caryopsis priming	• Increased K$^+$, Ca^{2+}, and decreased Na$^+$ and Cl$^-$ in both shoot and root • Improved PM permeability • Remarkably reduced lipid peroxidation • Increased GB accumulation and improved ion homeostasis	Salama et al. [94]
S-24 and MH-97	15 dS m^{-1} NaCl, 47 d	50 and 100 mM GB, foliar spray	• Modulated activities SOD, CAT, and POD • Significantly increased K$^+$/Na$^+$ ratio in leaves and roots, and Ca^{2+}/Na$^+$ ratio in leaves • Enhanced endogenous GB and K$^+$	Raza et al. [76]

Table 3. Protective effects of various exogenously applied osmoprotectants under salt stress in *T. aestivum*.

Priming of *T. aestivum* seeds with choline (5 and 10 mM) reduced the damaging effects of NaCl (150 mM) by increasing the K$^+$, Ca^{2+}, GB accumulation, improved ion homeostasis and decreased Na$^+$ and Cl$^-$ in both shoot and root, mitigated PM permeability and reduced lipid peroxidation of leaf [94]. Expression of *mtlD* gene encoding mannitol-1-phosphate dehydrogenase resulted in enhanced salt stress tolerance in *T. aestivum* due to defensive roles of mannitol against salt stress [95]. The *mtlD* gene encoding mannitol-1-phosphate dehydrogenase transformation in *T. aestivum* cv. Giza 163 conferred salt stress tolerance by inducing mannitol and reducing sugars in tissues of plant [96]. Kerepesi et al. [97] demonstrated that increased fructan contents in salt resistant (Sa) and moderately salt-tolerant (Ch) varieties of *T. aestivum* showed increased tolerance against salt stress (200 mM NaCl). Sharbatkhari et al. [98] investigated the role of fructan in salt-tolerant (Bam) and salt-sensitive (Ghods) cultivars of *T. aestivum*. They found higher fructan accumulation and remobilization in salt-tolerant Bam cultivar, which contributed to the higher salt stress tolerance by increasing the photosynthetic capacity and decreasing the salt induced severe yield loss.

4.2. Plant hormone

Plant hormones are chemicals produced within the plants at low concentration involved in regulation of plant development and tolerance towards various stresses including salinity [99]. Now-a-days, various kinds of plant hormones such as ABA, auxin, cytokinins (CK),

brassinosteroids and GA_3 are externally used for alleviating various kinds of abiotic stresses including salinity (**Table 4**). The plant growth hormone auxin increased the germination percentage, shoots DW and maintained ion homeostasis under salt stress condition [100]. Iqbal and Ashraf [101] reported that seed priming with different auxins alleviated salt stress (15 dS m^{-1}) by maintaining hormonal balance and assimilation rate and improved growth and yield of both tolerant and sensitive cultivars under salt stress condition. Seed priming with GA_3 alleviates the drastic effect of salinity and increases grain weight and grain quality by improving photosynthetic pigments, leaf area and plant growth [102]. Foliar application of GA_3 also confers salt stress tolerance by increasing germination percentage, plant growth and upregulating antioxidant enzyme [103]. Seed priming with cytokinin such as kinetin and benzylaminopurine (BAP) increase germination percentage and grain yield by increasing plant growth, productive tiller and 1000-grain weight under salt stress condition [104, 105]. Gurmani et al. [106] noted that, seed priming with ABA improved salt stress tolerance by increasing net assimilation rate, chl content and decreasing Na uptake. It is also evident that phytohormone brassinosteroid plays role in alleviating salt stress. Ali et al. [107] reported that brassinosteroid increased grain yield by improving photosynthetic attribute, assimilation rate and transpiration rate under salt stress condition (150 mM NaCl). Eleiwa et al. [22] also showed brassinosteroid-induced positive response in wheat seedlings under salt stress conditions (**Table 4**).

Cultivars	Salinity dose and duration	Dose of phytohormones	Protective effects	References
MH-97 (salt intolerant), Inqlab-91 (salt tolerant)	(15 ds m^{-1}) 150 mM NaCl, entire growth period	Auxin (Tryptopan) 4.89 × 10^{-4} mM, 12 h seed priming	• Increased CO_2 assimilation rate • Increased net assimilation rate • Increased growth • Increased productive tiller and grain yield	Iqbal and Ashraf [44]
MH-97 (salt intolerant), Inqlab-91 (salt tolerant)	150 mM NaCl, entire growth period	4.89 × 10^{-1} mM auxin (tryptophan), 12 h seed priming	• Increased germination percentage • Improved ion homeostasis • Increased shoot DW	Iqbal and Ashraf [100]
Sohag 3 (sensitive), Giza 168 (tolerant)	50, 100, 150, and 200 mM NaCl),entire life cycle	150 mg L^{-1} GA_3, foliar spray	• Improved leaf area, photosynthetic pigment, carobohydrate, protein, amino acid and Pro content, grain weight	Shaddad et al. [102]
MH-97, Inqlab-91	15 dS m^{-1}, 8 d	100, 150 and 200 mg L^{-1} cytokinins (kinetin and BAP), 12 h seed priming	• Increased germination rate • Increased early seedlings growth such as shoot DW and root DW	Iqbal et al. [105]
MH-97, Inqlab-91	15 dS m^{-1}, entire life cycle	100, 150 and 200 mg L^{-1} cytokinins (kinetin and BAP), 12 h seed priming	• Increased plant height, shoot dry biomass • Increased fertile tiller, 1000-grain weight, grain yield	Iqbal and Ashraf [104]

Cultivars	Salinity dose and duration	Dose of phytohormones	Protective effects	References
Mehran-89	0.13 M NaCl, 8 d	10^{-6} M ABA, 8 d	• Increased germination percentage, and shoot and root biomass	Naqvi et al. [108]
Kharchia-65, PUNJAB-85	100 mM NaCl 16 d	10 mM ABA, seed priming 24 h	• Increased plant height, root length • Improved root and shoot dry weight • Increased chl content • Increased net assimilation rate • Decreased Na uptake	Gurmani et al. [106]
Giza 164	2000–6000 ppm NaCl, irrigation water entire life cycle	0, 50, 100 and 200 mg L^{-1} 28-homobrassinoloide, foliar application,	• Increased chl, carotenoids and total pigments • Increased plant height, leaf area • Improved tiller number, weight of 1000 grain, grain yield and biological yield	Eleiwa et al. [22]
S-24, MH-97	150 mM NaCl, 45 d	0, 0.052, 0.104, 0.156 μM 24-epibrassinolide	• Increased photosynthetic attribute and chl content • Increased net CO_2 assimilation rate, stomatal conductance and transpiration rate • Increased root and shoot weight and length • Increased number of grain plant^{-1} and grain yield	Ali et al. [107]

Table 4. Protective effects of various exogenously applied phytohormones under salt stress in *T. aestivum*.

4.3. Plant nutrient

Along with other physiological and biochemical functions, plant nutrients play positive roles in alleviating damage effects of abiotic stresses including salinity (**Table 5**). Exogenous application of K enhanced salt stress tolerance in wheat seedlings by improving photosynthetic pigments, antioxidant enzyme activity, K uptake and decreasing Na uptake [109, 110]. Foliar application of phosphorus (P) also alleviated salt-induced damage by increasing plant biomass, leaf area and decreasing Na uptake [111]. Application of $CaSO_4$ increased plant growth, water status and K and Ca uptake under salt stress condition [112]. Later on, Tian et al. [113] noted that application of $Ca(NO_3)_2$ reduced salt-induced oxidative damage by decreasing lipid peroxidation and electrolyte leakage in wheat seedlings.

Cultivars	Salinity dose and duration	Plant nutrients	Protective effects	References
NAYAB-11 and MILLAT-11	150 mM NaCl, 113 d	50, 100, 150 and 200 mM K_2SO_4, 106 d	• Increased root length and biomass • Increased plant height and biomass • Increased K^+ uptake and decreased Na^+ uptake	Kausar and Gull [110]
Gemiza 9, Sakha 93	40, 80, and 120 mM NaCl, 90 d	25 and 150 mg K_2O kg^{-1} soil, 110 d	• Increased plant height and biomass • Increased chl *a*, chl *b* and carotenoid content • Increased SOD and POD activity	El-Lethy et al. [109]
	150 mM NaCl	400 and 800 mg P L^{-1}, foliar application	• Increased plant height, root length, root and shoot biomass • Increased leaf number, leaf area and chl content • Decreased Na uptake and increase K uptake	Khan et al. [111]
PUNJAB-85	50 mM NaCl, 34 d	3 and 6 mM $CaSO_4$	• Increased root and shoot biomass • Increased root and leaf RWC • Increase K and Ca uptake	Zaman et al. [112]
Jimai 22	100 mM NaCl, 15 d	17.5 mM $Ca(NO_3)_2$, 15 d	• Decreased $O_2^{\bullet-}$ and H_2O_2 contents • Decreased lipid peroxidation, electrolyte leakage • Increased SOD, POD, and CAT activities	Tian et al. [113]

Table 5. Protective effects of plant nutrients under salt stress in *T. aestivum*.

4.4. Antioxidant

Antioxidants are important for plants to maintain the ROS level lower. Plant possesses various non-enzymatic antioxidants in their cellular components to protect themselves from oxidative stress. The major antioxidant includes AsA, GSH, tocopherol and some phenolic compounds. Some of these antioxidants showed advanced protection against salt-induced oxidative stress when they were applied exogenously (**Table 6**). However, these are mostly dose dependent. A number of studies have been reported the positive effects of AsA in mitigating salt stress in wheat. Athar et al. [20] studied the effect of AsA on wheat plants subjected to salt stress. Salt stress (150 mM NaCl) caused reduction in growth and photosynthesis which were associated with decrease in tissue K^+/Na^+ ratio in both sensitive and moderately tolerant varieties. However, root applied AsA (100 mg L^{-1}) counteracted the adverse effects of salt stress on the growth of tolerant variety which was due to the

enhanced endogenous AsA level and CAT activity, and higher photosynthetic capacity, and accumulation of K^+ and Ca^{2+} in the leaves. Their study supports the notion that exogenous AsA counteracts the adverse effects of salt stress on growth of wheat by improving photosynthetic capacity of wheat plants against salt-induced oxidative stress and maintaining ion homeostasis, however, these effects were cultivar specific [20]. Ascobin (compound composed of ascorbic acid and citric acid) was found to be effective in mitigating salt-induced damages in wheat as reported by Elhamid et al. [114]. Salt stress markedly increased the lipid peroxidation while the activities of antioxidant enzymes (SOD, CAT, POD, APX and GR) dramatically increased. However, foliar treatment of wheat cultivars with ascobin could partially alleviate the harmful effect of salinity especially at the lower levels of salinity imposed in the two cultivars of wheat at most of the studied parameters [114]. Apart from the dose, mode of application is also a factor to initiate the protective effect by exogenous AsA. In their study Athar et al. [115] found differential effects when AsA was applied through the rooting medium, or as seed soaking or as foliar spray to salt stressed (120 mM NaCl) wheat plants. Exogenous AsA mitigated the adverse effect, e.g. improved leaf ascorbic acid, activities of CAT, POD, and SOD. Root applied AsA caused more enhancements in photosynthetic capacity and more reduction in leaf sodium (Na^+) compared with AsA applied as seed soaking or foliar spray. However, the effects were also cultivar specific [115]. In a hydroponic experiment Khan et al. [116] showed that foliar applied AsA (50 and 100 mg L^{-1}) could not alleviate the adverse effects of salt stress on plants, but it improved the growth of nonstressed plants. Since AsA failed to enhance the antioxidant defense, it enhanced the Na^+ accumulation in the leaves but did not change the K^+ accumulation in the salt-stressed plants. Azzedine et al. [21] observed that the exogenous AsA improved the plant growth under salt stress condition which was partly due to the increased leaf area, improved chl and carotenoid contents, enhanced Pro accumulation, and decreased H_2O_2 content. Melatonin (N-acetyl-5-methoxytryptamine) is also considered a potential antioxidant in plants which is distributed in many parts of the plant. Due to its universal hydrophilic and hydrophobic nature and solubility in both water and lipid, it can cross cell membranes easily and enter subcellular compartments and hence, considered as an antioxidant and a modulator in multiple plant developmental processes and various stress responses [117]. In their pot experiment, Sadak et al. [117] observed that wheat seeds presoaked with melatonin (100 and 500 μM) provided better growth, photosynthetic pigments, yield, and quality in wheat under salinity (3.85 and 7.69 dS m^{-1}). Melatonin treatments at different levels caused significant increase in yield and yield attributes, carbohydrate, protein, N, P, K, flavonoids, phenolic contents, and antioxidant activity either in nonstressed and salinity-stressed plants relative to their corresponding controls. Importantly, 500 μM melatonin was more effective than 100 μM. Farouk [118] reported that both AsA and α-tocopherol minimized salt-induced senescence of flag leaves of wheat. This was due to enhanced activities of antioxidant enzymes which led to the lower lipid peroxidation and H_2O_2 accumulation. Exogenous antioxidants also decreased membrane permeability, Na and Cl content. These higher levels of antioxidants and lower level of H_2O_2 in flag leaf might be the prerequisite for delayed leaf senescence in antioxidants-sprayed plants [118].

Cultivars	Dose and duration of stress	Antioxidants	Major effects	References
S-24 and MH-97	150 mM NaCl, 58 d	50, or 150 mg L^{-1} AsA	• Decreased Na$^+$ content, and increased K$^+$ and Ca^{2+} content • Improved photosynthesis • Increased AsA content and CAT activities • Improved growth	Athar et al. [20]
Sids 1 and Giza 168	3000 and 6000 mg L^{-1} NaCl, 75 d	200-600 mg L^{-1} ascorbin (ascorbic acid and citric acid 2:1)	• Decreased MDA content • Decreased activities of antioxidant enzymes	Elhamid et al. [114]
S-24 and MH-97	120 mM NaCl, throughout the growth duration	100 mg L^{-1} AsA	• Increased activities of CAT, POD, and SOD • Improved photosynthesis • Decreased Na$^+$ content	Athar et al. [115]
S-24 and MH-97	150 mM NaCl, 4 weeks	50 and 100 mg L^{-1} AsA	• Lower Na$^+$ accumulation • Protection of photosynthesis machineries	Khan et al. [116]
Waha	150 mM NaCl, 2 weeks	0.7 mM AsA	• Increased leaf area • Improved chl and carotenoid contents • Enhanced Pro accumulation • Decreased H$_2$O$_2$ content	Azzedine et al. [21]
Giza 168	0.23, 3.85, and 7.69 dS m^{-1} salinity, 75 d	500 μM melatonin	• Improved shoot height, number of leaves per plant, FW and DW of shoot • Increased photosynthetic pigments • Increased carbohydrate, protein, N, P, K, flavonoids, phenolic contents, and antioxidant activity	Sadak et al. [117]
Giza 168	0.8, 7.5, and 11.5 dS m^{-1} salinity, 65 d	100 mg L^{-1} AsA or α-tocopherol	• Enhanced antioxidant enzymes activities • Reduced H$_2$O$_2$ accumulation, lipid peroxidation, and membrane permeability • Decreased Na$^+$ and Cl$^-$ contents	Farouk [118]
Huaimai 17	300 mM NaCl, 7 d	100 μM SNP (sodium nitroprusside, a nitric oxide/NO donor)	• Improved germination • Deceased Na content and increased K content • Enhanced CAT and SOD activities	Zheng et al. [119]

Cultivars	Dose and duration of stress	Antioxidants	Major effects	References
S-24	150 mM NaCl, 2 weeks	0–150 μM SNP	• Increased FW • Increased leaf area • Increased photosynthetic parameters	Kausar and Shahbaz [120]
Pradip	100–200 mM NaCl, 48 h	1 mM SNP	• Decreased MDA and H_2O_2 content • Increased AsA and GSH content • Enhanced activities of antioxidant enzymes • Increased activities of glyoxalase enzymes	Hasanuzzaman et al. [24]
Sakha	2000–8000 ppm NaCl, 75 d	1.25–5.0 mM Arg (arginine)	• Decreased growth • Decreased yield components • Decreased grain and straw yield • Lower amount of Pro, secondary metabolites and mineral contents	Qados et al. [121]
Sepahan and Neyshabour	100 and 200 mM NaCl, 41 d	0.5 and 1.0 mM Spm	• Increased chl content • Enhanced antioxidant enzymes' activities	Saeidnejad et al. [122]
Zhengmai No. 004	150 mM NaCl, 48 h	0.05 μM H_2O_2	• Increased activities of SOD, CAT, APX, and POD • Increased AsA and GSH level • Decreased MDA and $O_2^{\bullet-}$ level • Improved plant height and biomass	Li et al. [123]

Table 6. Protective effects of various exogenously applied antioxidants under salt stress in *T. aestivum*.

4.5. Signaling molecules

Although there are specific signaling roles of phytohormones and antioxidants present in plants, which have been discussed in previous sections, this part will discuss the role of exogenously applied signaling molecules. Among the signaling molecules, nitric oxide (NO) has been widely studied in recent decades, due to its diverse role in tolerance to several abiotic stresses including salinity. Nitric oxide exerts its signaling role through various pathways and through interaction with other molecules (**Figure 3**) [26]. In the last decade, exogenous application of NO through different donors was found to enhance crop growth and productivity under stressful conditions [26]. Zheng et al. [119] observed great improvement in seed germination of wheat under high salinity (300 mM NaCl). Wheat seeds soaked in SNP solution provided better germination under salinity which was associated with decreased Na$^+$ concen-

tration and increased K^+ concentration in the seeds. Exogenous SNP also helped in increasing starch and amylase content in seeds which increased the weights of coleoptile and radical. Moreover, exogenous NO enhanced the activities of SOD and CAT which decreased the oxidative damages evident with lower level of lipid peroxidation, $O_2^{\bullet-}$, and H_2O_2 [119]. Kausar and Shahbaz [120] found the positive effect of foliar applied NO in mitigating salt stress in wheat. Wheat seedlings grown under 100 mM NaCl exhibited reduced growth and photosynthetic rate. However, NO spray ameliorated the effect by enhancing FW of plants, leaf area, stomatal conductance, and internal CO_2 concentration. However, NO could not take part role in enhancing PS II activity [120]. In our laboratory, we examined the effect of exogenous NO in conferring salt stress tolerance in wheat [24]. Wheat plant exposed to any level of salt (150 and 300 mM NaCl) caused significant increase in oxidative stress (as indicated by MDA and H_2O_2 content). Salt stress-induced oxidative stress was due to the disruption of antioxidant defense. However, the seedlings which were pretreated with NO donor (1 mM SNP) showed enhanced tolerance which was due to increased nonenzymatic antioxidants (AsA and GSH pool) and the activities of monodehydroascorbate reductase (MDHAR), DHAR, GR, glutathione S-transferase (GST), GPX, glyoxalase (Gly) I, and Gly II. Therefore, we concluded that both antioxidant defense and glyoxalase systems worked together in enhancing salt stress tolerance as induced by NO [24]. As shown in **Figure 3** Arg is one of the precursors of NO production. Few studies have indicated the role of exogenous Arg in salt stress tolerance in wheat. Qados et al. [121] observed that Arg could alleviate the salt-induced adverse effects in wheat. When wheat plants were exposed to different levels of salinity (2000–8000 ppm NaCl), plant mass, relative water content, yield components (spike length, spike weight, and spikelets per spike), grain yield, straw yield, biological yield, and harvest index decreased in dose dependent manners. Salt stress also deteriorated the chemical constituents of the grains. However, when the grains were presoaked with Arg, they provided better growth, yield components, yield as well as the quality aspects (nutrient content) at harvest [121]. Polyamines are often considered as signaling molecules which interact with NO and also exert direct beneficial effects [124–126]. Saeidnejad et al. [122] found the positive effect of spermine (Spm) in mitigating salt stress (100 and 200 mM NaCl) effect in wheat. In general, although seed priming with Spm showed a slight effect on germination process on both susceptible and tolerant cultivars, Spm application was an effective approach in salinity tolerance induction of wheat cultivars mostly through the activation of enzymatic antioxidants and increasing osmolytes production [122]. H_2O_2, which was previously thought to be a toxic substance and a major ROS recently been considered as signaling molecules. The double role of H_2O_2 is now an interesting topic of research of many plant scientists. However, as exogenous application, most of the experiments were conducted using H_2O_2 as priming agents or pretreatments rather than using as cotreatment. Signaling cross talk of H_2O_2 with NO is also well established since last two decades [127]. Exogenous H_2O_2 protected wheat plants from salt-induced damages by enhancing antioxidant defense as reported by Li et al. [123]. The seedlings supplemented with H_2O_2 (0.05 µM) decreased the levels of MDA and $O_2^{\bullet-}$, which was associated with the increased activities of SOD, POD, CAT and APX and the concentration of GSH and carotenoid under salt stress (150 mM NaCl). Exogenous H_2O_2 also increased plant height, shoot length, root length, and biomass under saline condition. The results were reversed when H_2O_2 scavenger was used that indicated a clear role of H_2O_2 in initiating its signaling role when applied at lower concentration [123].
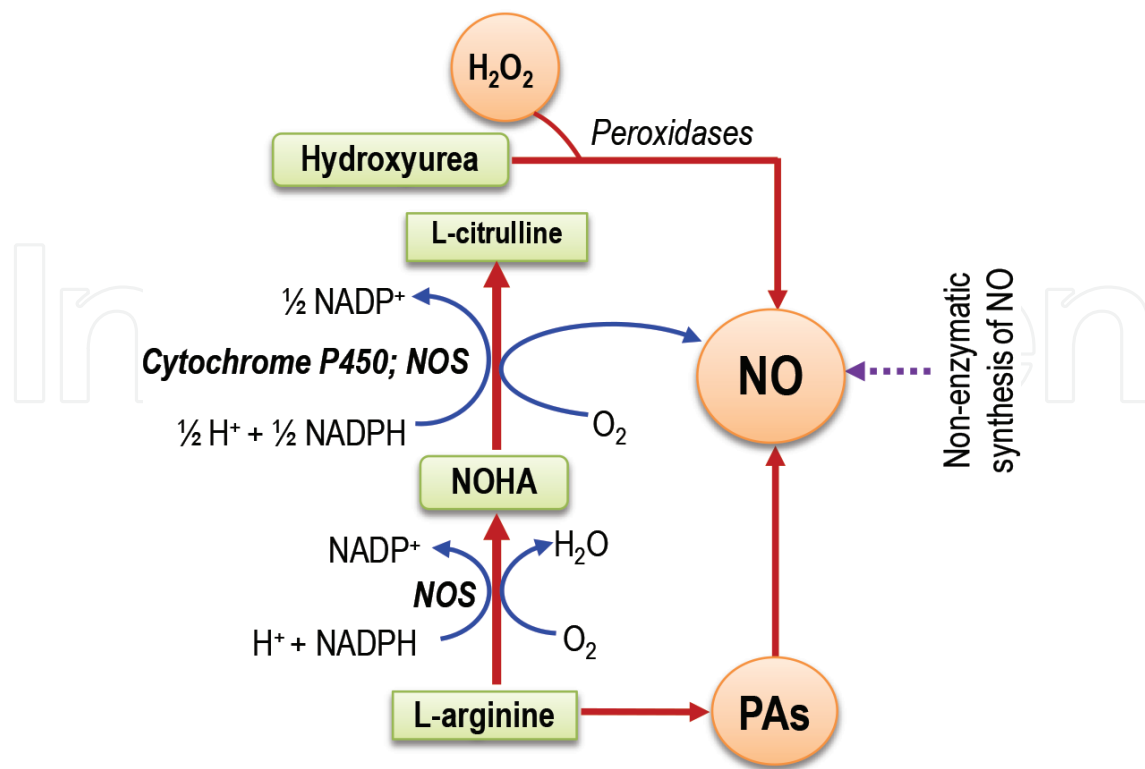
Figure 3. Interaction with PA, H_2O_2, and Arg during NO biosynthesis.

4.6. Seed priming

Seed priming is one of the easiest and cheapest techniques for successful crop production under various abiotic stress conditions including salinity [128, 129]. Seed priming is a presowing, controlled hydration technique that regulates and increases pregermination metabolic activity during early germination stage, but before radical projection [130, 131]. Seed priming has been effectively affirmed to improve germination percentage and seedling establishment in many crops such as wheat, rice, maize, soybean, canola, sunflower, sugarbeet, etc. [29, 132, 133]. Positive effects of seed priming might originate from de novo synthesis of certain germination-promoting substances, enhancing pregermination metabolites [131], early DNA replication, greater ATP availability, enzyme activation, osmotic adjustments [134], and membrane reorganization through restoring their original structures and reducing leakage of metabolites. Along with synchronous and fast emergence, primed seeds show reduced photo and thermodormancy, a wider range of germination temperatures and better capacity to compete with weeds and pathogens [135, 136]. Seed priming can be an easy solution for crops to overcome adverse environmental situations; it is reliable, simple, low cost, and also low risk technique [128, 137]. Various priming techniques such as hydropriming (soaking seed in water), osmopriming (soaking seed in nutrient, hormone, or chemicals), and halopriming (soaking seed in salt solution) have been developed to increase speed of germination, uniform seedling establishment, and crop production [138].

Seed priming has been effectively shown to increase germination and emergence of seeds of many crops in the tropical and subtropical areas, especially under salt stress conditions [139]. Increased germination rates and better seedling establishment resulted in higher levels of salt stress tolerance and crop yields when seeds were primed. Seed priming has recently been applied to overcome the salt stress problem on agricultural land [137]. Several research findings evidenced the role of seed priming to improve salt stress tolerance in wheat (**Table 7**). Hydropriming for 12 h on six Indian wheat cultivars showed 50% reduction of mean germination time under saline condition [140]. Effect of hydropriming was studied in salt-sensitive (MH-97) and salt-tolerant (AUQAB-2000) cultivars of wheat under salt stress (15 dS m^{-1}) condition [16]. It is well documented that seed osmopriming helps to improve salt stress tolerance in wheat seedlings. Seed osmopriming with PEG-8000 solution showed increased germination percentage, germination index, root and shoot length, and seedling FW and DW than salt-affected wheat seedlings at different salinity levels (4, 8, 12, and 16 dS m^{-1}). It has been reported that seed osmopriming with AsA helped to increase the endogenous AsA content and CAT activity which increased the salt stress tolerances in wheat [141]. Increased germination percentage, early seedling establishment, accumulation of ABA and Pro, and plant growth were featured due to seed osmopriming with 0.05 mM SA in wheat under salt stress condition [142]. Seed halopriming improves plant salt-tolerance by maintaining ion homeostasis mechanism. Salt stress increases the accumulation of Na$^+$ concentrations in the roots and shoots of wheat plants and decreases the uptake of beneficiary nutrients. However, seed halopriming helps to maintain the ion homeostasis by decreasing Na$^+$ concentration and increasing K$^+$, Ca^{2+} concentration, and K$^+$/Na$^+$ ratio in roots and shoots. Increasing K$^+$ and Ca^{2+} absorption, K$^+$/Na$^+$ ratio due to seed halopriming under salt stress was connected with vigorous seedling growth and crop production, increased photosynthetic activity, and reduced electrolyte leakage. Seed halopriming with CaCl$_2$ helps in the maintenance of ionic balance by reducing the Na$^+$ and increasing the K$^+$ absorption consequently improves salt stress tolerances [143]. Salt stress also induced oxidative damage by producing ROS. Seed halopriming detoxifies the ROS by increasing the activity of enzymatic antioxidant such as SOD and CAT [43]. Iqbal and Ashraf [100] demonstrated that halopriming with 100 mM KCl, NaCl, and CaCl$_2$ reduced the salt stress affect on growth and grain production of two wheat cultivars. Priming with phytohormone increased germination with better seedling establishment and tolerance to various stresses including salinity. Seed priming of wheat with IAA increased germination percentage by improving amylase activity [144] and mitigated the growth inhibitory effect of salinity [16]. Seed priming of three wheat cultivars with auxin (0, 1, and 2 mg L^{-1}) increased germination percentage, root and shoot length, seedling FW and DW, and yield under salt stress condition [18]. Priming with SA (100 mg L^{-1}) solution for 24 h enhanced growth, photosynthetic pigments such as chl a, chl b and also increased total soluble and reducing sugar for maintaining osmotic adjustment during salt stress [145]. Iqbal and Ashraf [101] reported that seed priming with GA (150 mg L^{-1}) played a potential role in alleviating salt stress damages by reducing Na$^+$ and Cl$^-$ concentrations, Na$^+$/K$^+$ ratio, and increasing K$^+$ and Ca^{2+} contents. Moreover, seed priming with GA increased germination percentage, seedling growth and yield contributing components under salt stress condition.

Cultivar	Priming agent	Duration of priming	Salinity doses and duration	Major responses	References
AUQAB-2000, MH-97	Hydropriming, 50.0 mM CaCl$_2$. 2H$_2$O, 50 mg L^{-1} AsA	Seeds soaked for 12 h	15 dS m^{-1}, 12 d	• Increased germination percentage • Reduced mean germination time • Increased root and shoot FW and DW • Enhanced activities of CAT, SOD, and POD	Afzal et al. [43]
Gomeza 7	25, 50, and 100 mM GB	Seed soaked for 24 h	150 mM NaCl, 38 d	• Decreased lipid peroxidation • Increased PM stability and eventually ion homeostasis	Salama et al. [88]
MH-97	1, 40, 80, and 120 μM H$_2$O$_2$	Seed soaked for 8 h	150 mM NaCl	• Increased photosynthetic capacity • Enhanced the leaf gas exchange • Increased K$^+$/Na$^+$ ratio	Wahid et al. [35]
	0.6 mM AsA and sodium salicylate, 0.3 mM thiamine	Seed soaked for 6 h	40, 80, 120, and 160 mM NaCl, 30 d	• Stimulated starch accumulation • Inhibited production of soluble protein • Reduced water soluble Pro accumulation	Al-hakimi and Hamada [141]
Gomeza 7	5 and 10 mM choline chloride	Seed soaked for 24 h	150 mM NaCl, 21 d	• Increased stigmasterol • Decreased cholesterol and campesterol • Increased the plasma membrane stability	Salama et al. [146]
AUQAB-2000	10 ppm ABA, 50 ppm SA, 50 and 100 ppm AsA	Seed soaked for 12 h	15 dS cm^{-1}	• Increased seed germination time • Decreased electrolyte leakage by modulating antioxidant enzymes	Afzal et al. [147]
AUQAB-2000	25 ppm IAA, 50 ppm GA$_3$, 100 ppm kinetin, and 1% prostart	Seed soaked in IAA, GA$_3$, and kinetin for 12 h; and in prostart for 2 h	15 dS cm^{-1}, 21d	• Decreased electrolyte leakage • Increased invertase, α-amylase and starch synthetase activities which helped in better seedling growth	Afzal et al. [16]
PUNJAB-11	10, 20, 30, 40, and 50 mM Na$_2$SiO$_3$	Seed soaked for 12 h	15 dS cm^{-1}	• Reduced accumulation of Na$^+$ • Increased Ca^{2+} content • Increased germination percentage, and root and shoot length • Vigorous seedling establishment	Azeem et al. [148]
DK961	0.06 mM SNP	Seed soaked for 24 h	100 mM NaCl	• Increased germination percentage by increasing α-amylase, β-amylase isoenzymes activities • Decreased MDA content, Na$^+$ content • Increased SOD, CAT, APX activities	Duan et al. [149]

Cultivar	Priming agent	Duration of priming	Salinity doses and duration	Major responses	References
Kakaba and Paven-76	1 and 2% $CaCl_2$ and KNO_3	Seed soaked for 12 h	5.97, 9.62, 13.28, and 16.9 dS m^{-1}	• Increased germination with uniform seedlings • Increased tillers per plant • Shortened the physiological maturity period	Dugasa et al. [150]
Tatara-96, Ghaznavi-98, Fakhri Sarhad, Bakhtawar-92, Pirsabaq-2004 and AUQAB-2000	30 mM NaCl	Seed soaked	0, 40, 80, and 120 mM NaCl, 55 d	• Enhanced the activities of enzymatic antioxidants • Maintained ionic balance by increasing K$^+$ and Ca^{2+} accumulation • Increased tillers per plant and grain yield	Jamal et al. [32]
MH-97, Inqlab-91	100, 150, and 200 mg L^{-1} kinetin and BAP	Seed soaked for 12 h	15 dS m^{-1}	• Increased germination and early seedling establishment • Increased shoot dry weight and grain yield • Enhanced the endogenous growth hormones • Maintained hormonal homeostasis	Iqbal et al. [105]
MH-97, Inqlab-91	100, 150, and 200 mg L^{-1} GA$_3$	Seeds primed for 12 h	15 dS m^{-1}	• Maintained ionic balance by decreasing Na$^+$ and Cl$^-$ ions in roots and shoots • Increased Ca^{2+} and K$^+$ in roots and shoot • Increased leaf salicylic acid concentration • Increased fertile tiller per plant and grain yield	Iqbal and Ashraf [101]
MH-97, Inqlab-91	2.5 mM Spd and 5 mM Spm	Seeds soaked for 12 h	15 dS m^{-1}	• Increased shoot growth and grain yield • Enhanced beneficial mineral nutrient uptake by maintaining ion homeostasis • Increased biomass production and photosynthesis rate	Iqbal [151]
Inqlab-91 and SARC-1	50 mM NaCl, $CaCl_2$, and $CaSO_4$	Seeds soaked for 12 h	125 mM NaCl	• Increased germination percentage by increasing total soluble and reducing sugar • Increased shoot and root length under $CaCl_2$ and $CaSO_4$ priming • Increased biomass production • Improved K$^+$ and Ca^{2+} accumulation, and reduced Na$^+$ concentration	Afzal et al. [28]

Cultivar	Priming agent	Duration of priming	Salinity doses and duration	Major responses	References
SARC-1 and MH-97	50 mg L^{-1} AsA, CaCl$_2$, kinetin, and SA	Immersed seed in solutions for 12 h	20 dS m^{-1}	• Decreased emergence time by inducing biochemical changes and antioxidant enzymes activity • Reduced Na$^+$ absorption, and increased K$^+$ and Ca^{2+} absorption • Improved protease and α-amylase activities • Enhanced all agronomic and yield characteristics such as plant height, number of tillers, number of spikelets, grain yield, biological yield, and harvest index	Jafar et al. [143]
Caxton	22% PEG-6000	Seed soaked for 6 h	50, 100, 150, and 200 mM of NaCl	• Improved germination related metabolic activity such as synthesis of nucleic acids, proteins, and enzymes, and enhanced respiratory activity upto 150 mM level of salt stress but at 200 mM salt stress priming effect becomes reduced	Fuller et al. [31]
Sakha-93, Gemmiza-9	0.2 mM SNP, 9% diluted sea water, diluted sea water + SNP	Seeds soaked for 10 h	9 dS m^{-1}	• Increased leaf pigment concentration • Enhanced membrane stability by decreasing lipid peroxidation • Increased total soluble sugar, K$^+$ and Ca^{2+} concentration which decreased Na$^+$ uptake	Maswada and Abd El-Kader [152]
Inqlab and S-24	100 mg L^{-1} SA	Seeds soaked for 24 h	50 or 100 mM NaCl; 14 d	• Increased root and shoot length, root and shoot dry weight, total soluble sugar, and carbohydrate metabolism • Increased chl a and b content	Hamid et al. [145]
Azar 2	3% NaCl, 5% mannitol, 25% sugar beet extract and hydropriming	Seeds soaked for 4, 8, and 10 h	3.6 dS m^{-1}	• Increased hypocotyle length, root number and leaf length, shoot and root fresh weight • Increased photosynthesis rate • Enhanced biomass production	Amoghein et al. [153]

Table 7. Beneficial effects of seed priming in improving salt stress tolerance in *T. aestivum*.

5. Conclusions and future perspectives

Wheat is the most popular and widely consumed cereal crops in the world due to its diverse uses. Most of the cultivated wheat is hexaploid which has some acquired tolerance to salt stress. However, increasing levels of salinity in irrigated lands make wheat production difficult because plant growth and productivity of wheat are severely affected by high salinity. Salt stress adversely

affects seed germination, plant growth, photosynthesis, water relations, nutrient uptake, and yield. Oxidative stress is one of the most common effects of salt stress in wheat. However, salt stress effects depend on the dose and duration of stress, and mostly on genotypes. Considering the importance of wheat and the adverse effects of salt stress, plant biologists are trying to develop strategies to improve salt tolerance in wheat. Some of the strategies are related to the genetic manipulation of salt-tolerant traits. Physiologists are also trying to find the adaptive mechanisms to cope with the salt stress. However, the actual physiological mechanism of salt stress tolerance is yet to be revealed. Therefore, coordinated attempts by plant physiologists, breeders, and agronomists are essential to find out a sustainable strategy to enhance salt tolerance in wheat.

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